XV.—*Coloration as a Factor in Family and Generic Differentiation.* By Percy R. Lowe, B.A , M.B., M.B.O.U.*.

I should like to state at once that in the few remarks which I propose to make on the subject of to-night's discussion, it is no part of my plan to attempt in any way to upset the established characters and methods which are employed in generic differentiation or to substitute for these some brand-new scheme based on colour-characters. Such a proceeding would be both futile and foolish. All I wish to accentuate is this—that colour-pattern seems to be a very important feature in generic differentiation, which has been, I cannot help thinking, unnecessarily neglected, looked down upon, or ignored. I believe not only that colour-pattern furnishes, in many instances, an important clue to the phylogenetic relationships of various groups of species, but that it would, if properly applied, enable us to get a practical and working idea of the limits of genera.

I believe, in a word, that the employment of the factor of colour-pattern in generic differentiation would act, in many instances, in the way, so to speak, of a control experiment by which we might either substantiate or correct previous estimates of generic groups which have been based on such characters as are usually employed.

Applied in a systematic way to all the genera which exist at the present time throughout the whole class of Birds, I cannot help thinking that many of these genera would be found either to include too many species or too few.

Finally, I do not for one moment hold the view that this factor can be universally applied to all genera, or anything like all; but where it can be used with good results, I can see no possible reason why it should not be applied—and applied, moreover, without fear of laying ourselves open to the charge of mere amateurism.

* * * * *

* A discourse delivered to the British Ornithologists' Club, February 10, 1915.

Before coming to the more practical side of the subject, it will be necessary to consider it from a general point of view, by way of clearing the ground and of trying to demonstrate how fundamentally important and how deep-seated colour-pattern is—that it is not the superficial and negligible character which it is generally held to be, and that the factors of environment play but a comparatively small and indirect part in its existence. The first point, then, which I should like to lay stress on is :

(1) **The distinction which must be made between "colour-pattern" and mere coloration.**

It will probably be generally admitted that there is a very great difference between the two. Colour-pattern (that is to say, a certain definite and more or less constant relation of colour-factors to certain definite areas of the contour-plumage, occurring through a series of species or genera) implies something of a deeper import than mere coloration—something which from its constancy and persistency, its independence of mere environmental or climatic influences, and its correlation with faunal or geographic areas, appears to undoubtedly suggest the influence of the germ-plasm. If this is so, it obviously follows that the factor of colour-pattern must be of genetic importance. It is heritable. It ought to be, as I believe in many cases it is, a useful phylogenetic guide or clue.

Mere coloration, on the other hand, may, I suggest, be regarded as somewhat akin to mere homoplastic variations or convergent adaptations in the deeper realms of morphology. Regarded in this sense, mere coloration of this kind is of no genetic value. Again, mere shades and tones of coloration, from the fact that they are the result of direct environmental effects or possibly, in some cases, of simple isolation, and moreover are often simply adaptative or procryptic, have likewise no genetic value. They appear to be exogenous in origin, physiological, ontogenetic and non-heritable. It hardly seems worth while to labour these points, but I must give an example or two to clear the ground.

The upper parts of Auks, Guillemots, and Shearwaters, for instance, are some dark shade of slaty-blue or black, and their underparts are white ; and this coloration has presumably been impressed upon them for the sole purpose of harmony with the elements in which they live ; but we may take it for granted that no ornithologist would attach the smallest importance to this resemblance in coloration from the point of view of relationship, or would conceive for one moment that the Shearwaters were related to the Auks—nor would it incline us of itself and by itself to include the Auks and Guillemots in the same genus.

Again, as regards mere depths of tones and shades of coloration, I may remind you, as an example of the superficial nature of such coloration, of the case of the European Goldfinch, which was introduced into the Bermudas somewhere about the year 1870.

These Finches have within this very recent historical period acquired such a very dark tint as regards their upper parts that Mr. Kennedy has not hesitated to differentiate them as a distinct subspecies.

It is very difficult to think that this phenomenon of coloration in the Bermudan Goldfinches is anything else than a superficial, physiological and non-heritable response to a change of environment or to mere segregation. It is a *fluctuational variation.*

But, on the other hand, reverting to the subject of colour-pattern, take the case of the Ringed Plover association. We are all familiar with the very constant type of colour-pattern characteristic of this very widespread and cosmopolitan group. We know that the head and breast of any one species exhibits in a more or less perfect condition a thoroughly stereotyped reproduction of the colour-pattern of any other species, no matter how many thousands of miles of ocean may separate them, and whether those species are found in the old or new worlds, or occur on the mainland or on isolated islands.

I will not detain you with any details of this colour-pattern; but what I want to emphasise here is this—Could anyone seriously imagine for one moment that this particular and constantly occurring colour-pattern was absolutely indispensable for the continued existence of this particular race of Plovers as contrasted with other races of Plovers, and from the point of view of an indispensable harmony with their environment, or ever had been so indispensable at any age or under any circumstances? The mere fact that such a stereotyped pattern is found in such varying types of environment as the peculiar plateau of St. Helena, the grassy velds of southern Africa, or the sandy shores of our own islands, surely suggests that its origin is not entirely a matter of concealing coloration or adaptative. On the contrary, may we not surmise that this particular colour-complex was a character or a colour-tendency which was impressed on these Ringed Plovers ages back, through the influence of some purely fortuitous shuffling of the chromosomes in the germ-cells of some remote ancestor? It is a colour-pattern or a colour-tendency which has persisted, not because it owed its origin to any formal plan for the protective concealment of these Plovers, but because the germ-cell, once started on a certain line, could not help repeating itself in this direction, and because, since the colour-tendency was not harmful to the race, there was no excuse for any eliminating factor to suppress either it or the race; and so the germ-cell, or the jugglery which takes place within it, has gone on repeating itself, and will go on repeating itself, until some sudden mutation or reshuffling of the chromosomes in the germ-cells of any particular individual of any species starts a new line of evolution in colour-pattern (a genetic variation or mutation).

In such a case, then, as the colour-pattern which is typical of the cosmopolitan Ringed Plovers, I submit that we have a colour-complex which is endogenous or genetic. It is congenital. It can be used as a generic test or character. But, of course, we have got to be on our guard in making use of colour-characters in classification; for just as in the case of deeper structural features we have to eliminate the homoplastic factor in cases of mere convergent likenesses, so in the case of these colour-pictures, if one may so term them, it is our business or the business of those who believe in the importance of coloration as a factor in generic differentiation, to distinguish between those which are simply cryptic or concerned in the business of concealment and those which are not so concerned.

One may, of course, have both types of coloration in any particular species. For instance, taking the Ringed Plover group again, no one would deny that the Kentish Plover is protectively coloured in an obliterative direction and in harmony with its usual sandy or arid environments. But this obliterative factor is merely an affair of shades and tones of coloration which are superimposed upon the fundamental colour-pattern characteristic of the genus. The mere depth of tones in desert situations is the direct outcome of the greater intensity of light and the increased aridity, while the tendency of the species in such environments to be invisible is the result of a nicely adjusted process of counter-shading, and both are the result of the reaction of the organism to its immediate surroundings. The fundamental colour-pattern is still there, although modified.

Any organism, in fact, not only reacts to outward stimuli but it has also an inherent power to *act* on, so to speak, its own initiative; and this is a fact that in the matter of this question of coloration we must not lose sight of. The fact that coloration or colour-pattern as a serious aid to classification in birds has been regarded with a certain amount of contempt and suspicion has, I take it, arisen from the supposition that all coloration or all colour-patterns are the direct outcome of the action of external factors—or, to put it shortly, that the coloration of birds is invariably cryptic and a mere superficial response to environment in the direction of enhanced invisibility.

(2) **The question of concealing coloration.**

Before, however, passing on to the consideration of colour-pattern as a phylogenetic or generic clue, which is the chief point of this discussion, I should like very briefly to notice one or two other aspects of the subject of coloration by way of still further clearing the ground, in the direction of trying to show that colour-pattern in the great majority of cases is endogenous or genetic in origin, and so enhancing its value as a character to be used in classification.

All sorts of pretty theories have been brought forward in connection with this aspect of the coloration of birds; but it seems to me that if concealing coloration was really such a universal phenomenon as it is often made out to be, we ought to find, as a general rule, that there was a far greater, a more universal, and a more intimate commingling of every kind of procryptic colour, irrespective of well-differentiated groups of birds *. Instead of this, we find that certain distinctive colour-schemes are characteristic and proper to certain families or genera of birds, quite irrespective of the fact that such families or genera are exposed to precisely similar environments. To be as brief as possible, one gets the impression, in trying to analyse the colour-factors characteristic of families or genera, that in such groups of birds the ancestral germ-cells had, so to speak, two or three colour-factors to "play with" and make the best of. All the germ-cell or the chromosomes could do was to produce variations with the particular colour-factors they had originally at their disposal. If these variations were not flagrantly inharmonious with their environment, all was well and good.

The accompanying diagram may serve to demonstrate at a glance the idea which I wish to advance. It has reference to the family Drepanididæ of the Hawaiian Islands, and, assuming with Dr. Starr Jordan † that *Oreomystes bairdi* (with its least specialised bill, its wider adaptative powers, its more ubiquitous distribution, and its neutral coloration as regards both sexes) is the most

* The colour-pattern of nestling Grebes and Moorhens is conspicuously different, although their environment is identical; and many other examples might be given both in the case of nestlings and adults.

† *Cf.* 'Science,' vol. xxii. 1905, p. 555. In this article Dr. Starr Jordan assumes this for another reason.

ancestral living representative of this group, we may suppose that this species stands at the point of divergence of the two branches into which this family seems to have split. In the germ-cells of this species or its ancestors there are or were presumably resident three potential colour-factors —red, yellow, and black (this last independently distributed); and out of these, the colour-scheme characteristic of any or all the genera of the family could be constructed by various combinations (in the direction of either addition or loss) of these primary colour-factors. Incidentally, it is somewhat tempting to suggest that there were also two factors for the form and shape of the bill—a *Pseudonestor*-bill factor and a *Drepanis*-bill factor.

In connection with this subject of particular groups of birds having particular colour-schemes, or having particular colour-factors proper to them, Mr. Witmer Stone* has recently called attention to the absence of red among the Jays or of green among the Thrushes. He has also called attention to certain conspicuous colour-patterns which it is difficult to reconcile with any plan for concealment or indeed with any scheme of a breaking-up or ruptive nature. For instance, he quotes the metallic blue or green speculum in the Ducks or the blue and black wing-patch in the Jays.

In making these remarks on this aspect of coloration, I am not, of course, trying to belittle the patent and manifest facts of concealing coloration, which seems obvious enough in certain groups of birds. I am not quarrelling with the theory of countershading as set forth by Thayer†;

* "The Phylogenetic Value of Colour-characters in Birds," by Witmer Stone, A.M., Journ. Acad. Nat. Sci. Philad. 2nd series, vol. xv. 1912, p. 314.

† If Thayer had done nothing else than accentuate the difference between how we see things with the brain and how we see them with the eye, he would not have written his very instructive book in vain. We have grown so accustomed to habitually see things with the brain that it is only the trained artist who, as a rule, and then only by a certain effort, can switch off his brain and see things *as they really look*, instead of in the way we are accustomed to translate them by means of our brain. Therefore, in thinking of questions like that of concealing-

nor am I saying that the pectoral bands on the breast of the Ringed Plover, or the peculiar pattern on its head, do not serve a useful ruptive purpose in helping to break up the continuity of its form. But what I *am* trying to maintain is that the idea of protective-coloration is a conception or even a hobby which is in danger of being ridden to death—that it is only one phase of the whole question of coloration, and that, taking the class of Birds as a whole, it has probably always been a more or less lucky chance, so to speak, if colour-pattern, born of genetic influences, happened to coincide with such a useful purpose as invisibility or concealment.

The idea in the past was that coloration or colour-patterns were invariably impressed on the bird's plumage from without, and hence systematists fought shy of using such characters in classification. But there is always the other side of the picture, namely, that birds, originally possessed of a certain type of colour-pattern, unconsciously suited themselves to certain types of environment ; and if they did not—Well ! there was always our old friend Natural Selection in the background and—they *disappeared.*

The Trogons occur to me as a good example of this other side of the picture, because I happen to have made the acquaintance of several species in their native haunts. The Trogon peculiar to Cuba, for instance, is in reality a very conspicuously coloured bird ; yet I have found it at times very difficult to find in the forests, although I happened to know that I was within a few yards of one from having heard its peculiar pheasant-like cry. The reason for this

---

coloration, we ought not to forget that our "brain-power" is of a very different order to the "brain-power" of a bird or a mammal. It is, for instance, more than possible that birds habitually see things *as they really look.* It is in the highest degree unlikely that the brain of a bird acts in the same way as ours in the direction of transforming the vision of what the eye really sees into a picture of what the brain chooses to think it sees, likes to think it sees, or has grown accustomed to think it sees.

was that the brilliant scarlet of its underparts was apparently confused with the scarlet inflorescence of certain arboreal and parasitic plants which were common. The Trogon had, in fact, unconsciously "adapted itself" to its scarlet-tinted surroundings; for it is to me quite an unthinkable proposition to suppose that these scarlet-coloured epiphytes could by any conceivable means have so affected the germ-cells of these Trogons that they were induced to respond in sympathy with their environment. Yet this is exactly what we are often asked to believe. On the contrary, the germ-cell produced the scarlet area and the Trogon has made, so to speak, the best of a bad job.

(3) **The constancy and persistence of colour-pattern.**

I have already referred incidentally to this in the case of the Ringed Plovers, in which we find that in spite of extreme isolating conditions and of differences in the type of environment, the fundamental colour-pattern remains the same. Not only is it persistent, but it is more constant than the structural features of the bills, in which we find a whole series of intergradations.

There is another example in the case of three distinct genera of Cuckoos from the East Indies, viz. *Dryococcyx* from Celebes, *Rhinococcyx* of Java, and *Urococcyx* from Sumatra and the Malay Peninsula. I have taken these examples from Mr. Witmer Stone's paper, and it will be noticed that while there are very distinct structural differences in the form of the nostril corresponding to the three genera, the colour-pattern remains the same. It seems to me quite inconceivable that this colour-pattern owes its origin to adaptation with environment, since if we compared the immediate environment of East Indian with, let us say, West Indian Cuckoos, the details would almost certainly be found to be so completely similar that we should expect to find a similarity of colour-pattern and colour-tones, which however and in fact we do not.

We have another instance in the series of the larger

Caciques or Oropendolas of the family Icteridæ*. In this series we have represented five genera, and, from the point of view of the structural features of the bills and other characters, I think it will be allowed that they are five genera as well-marked and distinct as any that could be found in any one group. Yet, as you will notice, the colour-pattern is fixed and absolutely characteristic.

There is another point which I must now briefly notice:

(4) The correlation of colour-pattern with geographical or faunal areas.

This seems to me an important side of the question, as not only showing that colour-pattern is a deep-seated phenomenon, but as pointing to the very secondary, if any, part which mere environment has played in its determination.

I propose to take the genus *Cœreba* as an example. Those members who are familiar with South American birds will remember that this genus of brightly-coloured Honey-Creepers can be divided into two groups, namely, a group with white spots on the wings, and a group without white wing-spots.

Here is a map illustrating the distribution of these two races †—the white wing-spotted race being represented in green, and the race without wing-spots in red.

Now, the two areas respectively occupied by these two races of *Cœreba* are, although now connected throughout the greater part of their extent, absolutely distinct in origin, and present entirely different geological features and history. The area coloured red, for instance, represents the extremely ancient and, at one time, insulated Brazilian and Guianan land-masses. It consists of the most ancient rock-systems known—Pre-Cambrian gneisses and Archean schists. On the other hand, the area coloured green consists almost entirely of Tertiary deposits which have been comparatively

* Examples of the following genera were exhibited, viz., *Clypeicterus*, *Eucorystes*, *Gymnostinops*, *Ostinops*, and *Ocyalus*.

† *Cf.* also 'Ibis,' July 1912.

recently upheaved so as to form the Peruvian and Columbian Andes, the Cordilleras of Venezuela, the Central American mountain ridge, and the interrupted rock-systems of the Greater Antillean islands. The rock-systems of the whole of this green area are, for all practical purposes, in almost complete geological continuity and, as compared with the rock-systems represented by the red area, are things of yesterday.

Now, I think it is pretty safe to conclude that the original centre of distribution of the genus *Cœreba* was represented by this red-coloured Brazilian land-mass. This seems indicated by the more generalised, more constant, and less differentiated nature of the colouring and colour-pattern of the race without white wing-spots. But assuming that the old Brazilian land-mass did indeed represent the original centre of distribution of the genus, we find that no sooner did the genus extend its area of distribution to the more recent land-areas, coloured green, than this factor of the white wing-spot became conspicuous and absolutely constant in the new area of occupation. It looks, indeed, as if the potentiality of the germ-cell, in the original and older race, to produce the white wing-spot had been held in check in the old area of distribution, but that the moment migration to a new and isolated area took place, this tendency of the germ-cell was unchecked or given free play. That there was a potentiality in this direction always resident in the germ-cell is, I think, indicated by the fact that every now and then, but still only in quite rare instances, indications of a white wing-spot crop up in the race without white wing-spots. In a large series of 70 specimens, for example, from Matto Grosso, Mr. Allen found a very small percentage.

It may be thought that this is a very long story about a very small thing; because, as anyone can see by examining these *Cœreba* specimens, the presence or absence of a white wing-spot in the two respective races seems a very trivial and almost contemptible circumstance. But it is just for this very reason of apparent triviality that I have used it as an example. For the point is this—could anyone possibly conceive that the presence of this white wing-spot in the one case, or its absence in the other, could serve any useful purpose, or the reverse? Could anyone possibly imagine that the white wing-spot had been directly impressed on the white wing-spotted race through the agency of external factors represented by a difference of environment? The idea is absolutely unthinkable; and the sooner we cease to practise any sort of self-deception in this direction the better. On the contrary, what this story of the genus *Cœreba*, thus briefly condensed, seems to prove is that colour-pattern is a deep-lying phenomenon, an affair of the germ-cell—a congenital manifestation. It owes its continued manifestation after its first inception to the effects of isolation and segregation. As such it cannot be the superficial and contemptible factor which it has been held to be.

I may add that the presence of the white wing-spot in the race inhabiting the green-coloured area is invariably constant, whether species possessing such a spot live at an altitude of 8000 or 9000 feet in the Peruvian Andes, or whether they are found in arid and sparsely vegetated country at dead sea-level, such, for instance, as is found in the very isolated Cayman Islands. In all these species mere depth of tone in coloration is very variable, as we might expect—the fundamental colour-pattern is constant.

To further accentuate the moral of this tale, I have here two pairs of nestling Plovers or Waders. In the one pair you see a nestling Stone-Curlew from our own islands (*Burhinus œdicnemus*) and another from Australia (*Burhinus magnirostris*); in the other pair a nestling Oyster-catcher (*Hæmatopus ostralegus*), again from our islands, and another nestling (*H. palliatus*) from America. In either pair the same identical details of colour-pattern are stereotyped with almost mechanical precision; and we are asked to believe that this precise identity of detail has been stamped upon each particular pair of nestling Plovers by a corresponding precision of identity in the immediate environment representing the respective "birth-places" of either of these two pairs of birds, widely separated as they are in the matter of both latitude and longitude. Even allowing that, in the case of the Stone-Curlews, the immediate environmental details of the Norfolk "Brecks" were precisely identical with those of the "Never Never Lands," or the arid plains of Australia, it is quite beyond our ordinary powers of conception to imagine how such a contingency could possibly have brought about such a marvellous and faithful replica of colour-pattern in two nestling species, separated as they are by the whole vast space occupied by the continent of Asia, and even although we allow an enormous amount of time for the action of Natural Selection in rejecting untold numbers of cases of the "unfit" which would not satisfy the equation.

In a word, it seems quite unthinkable that either environment or Natural Selection, or both combined, could directly affect the action of the germ-cells. We therefore come back to the statement previously made at the outset of these remarks, viz., that the germ-cells are the original designers of colour-pattern, that such colour-patterns are submitted to the approval of a committee formed by environment and Natural Selection, and if passed they persist. The "little by little" theory or the transmission of gradual accumulations of minute and favourable variations, acquired as the result of the influence of external factors during the life of any particular organism, and which favourable variations permit an ascendency over the parent stock, still remains a theory. In practice, we have absolutely no evidence to substantiate it. Even allowing, as seems evident and certain, that certain changes can be produced by environmental effects, "how can we suppose it in the smallest degree likely that very precise new and adaptative powers can be conferred on the germ-cells by such treatment" (Bateson, "Problems of Genetics"). The colour-pattern, then, in these two pairs of nestling Plovers is a deep-seated and important phenomenon. It owes its origin to the independent jugglery which went on in the germ-cells of the ancestral progenitors of the Stone-Curlews and the Oyster-catchers. From the original centre of distribution of those progenitors, the two races spread and radiated to occupy their present areas of distribution. They carried with them the legacy of the ancestral germ-cells.

How little environment has had to do with their colour-pattern, is indicated by the additional fact, that not only is the colour-pattern of the two nestling Stone-Curlews, from the two countries already mentioned, identical in detail, but their characteristic stripes and markings are also, for all practical purposes, identical with the like markings on the two Oyster-catchers already referred to; a fact which may and probably does indicate a community of descent or phylogeny, but certainly cannot be interpreted in the sense that the environmental details proper to these two forms are identical.

Returning however, to the more particular subject of the actual correlation of colour-pattern with geographical or faunal areas, many instances might be quoted. Mr. Witmer Stone has given, for example, the case of the three genera of eastern Cuckoos mentioned above; but I must limit myself here to one other example.

In the genus *Emberiza* we have a group of species (*E. flaviventris, poliopleura, major,* and *cabanisi*) from various African localities which have a distinctive colour-pattern, in which the factor of yellow is very prominent. In east Siberia, Manchuria, and Japan, we find two species of *Emberiza* (*E. elegans* and *chrysophrys*) in which although yellow plays a part, the colour-pattern is distinctly differentiated from the above. Both these groups are in turn differentiated from another group comprising such species as *E. cia, cioides, castaneiceps, ciopsis,* and *stracheyi.* My contention is, that the colour-pattern characteristic of such groups, not to mention others, must have a distinctive genetic import, which is independent of environmental effects and for which we ought, incidentally, to have some method of expression in our system of classification. We must in classification, work our way down to such natural compound units. (In this connection, see also remarks under

"The relationship of colour-pattern to genera-splitting and genera-lumping.")

Finally, so far as general considerations go, there is the question of

(5) **The relationship of colour-pattern to sex.**

It may be argued that the fact that the male is so often more brightly coloured than the female, is a difficulty which lessens the value of colour-pattern as a factor in generic differentiation. The female, too, as we all know, may in certain instances usurp the brighter plumage of the male. Mr. Rothschild has given me an instance, in the case of the genus *Oreomystes* of the family Drepanididæ, which he considers an example of the difficultics of applying the factor of colour as a generic character.

In *Oreomystes*, while the rule is that both male and female are green, we find in *O. flammea* that the male is all red and female not all red. Well, it seems to me that as far as I understand the problem, the fact that the male generally has a brighter and different colour-pattern from the female, or that the female may take on masculine characters, or that in any given genus the male of certain species may be found with an exceptional type of coloration, proves very little more than this, viz., that for some reason or other, some restraining factor which, as a rule, is operative in the female is not so operative in the male.

The fact that, in one species of the genus *Oreomystes*, the males are red instead of green simply points to the fact that in the *Oreomystes* germ-cell there was always a latent combination of factors, which at any moment might produce the factor of red, if given the chance; and I have already spoken of the way in which in certain families or groups of families we seem to see two conspicuous and contrasted colour-factors, or perhaps more than two, which are constantly turning up in the species of the group.

The moral seems to me to be that we must ignore the colour-factors of the male, or of the female if she has assumed masculine attributes, and take as our pattern the ancestral type of colour-picture, which is either generally fixed in the female or in the immature. From these general considerations, I now come to the more practical side of the question of colour-pattern as a factor in generic differentiation, and one of the points in this connection is :—

(6) The correlation of colour-pattern with other generic characters.

This point I shall dispose of very briefly, as it is so obviously self-evident, and my time is so short that I do not want to waste it in proving something which anyone can see by opening a series of drawers in the cabinets of the British Museum.

I do not say that colour-pattern is invariably so correlated, but, whether colour-pattern is used as a factor in generic differentiation or not, it is as a fact correlated in such an enormous number of instances that one cannot help being impressed. Consciously or subconsciously systematists seem in fact to have been guided by it.

Let me tell you the following story in illustration of this point. While looking for some good examples of this correlation of colour-pattern with generic groups, Mr. Ogilvie-Grant was kind enough to direct my attention to the Babblers—the Crateropodidæ.

I knew absolutely nothing about this group of birds, so that it is fair to say that I came to their study with no preconceived ideas on the genera. I approached the subject entirely from the point of view of colour-pattern, my only aids being the 'Catalogue of Birds' and Oates's well-known work. So far as my examination extended, I took as a pattern the type of each genus from the 'Catalogue of Birds,' and with those to guide me made a list of all the species which I considered ought to be included in each respective genus on colour-pattern alone. The result was that, so far as Indian birds were concerned, my genera were, as regards species, practically identical with Oates's. On the other hand, as regards the 'Catalogue of Birds,' I found myself constantly in disagreement. I found, for instance.

that a good many species which I should have thought worthy of generic distinction, from the point of view of colour-pattern, were not so considered in the 'Catologue of Birds,' but were included with other genera with a perfectly different colour-pattern. Well! to make a long story short, if Oates had not made new genera for these distinctively coloured species, someone else had.

Mr. Grant tells me that this group of birds used to be considered the dumping-ground for all doubtful forms whose classification presented difficulties—a sort of waste-paper basket for puzzled or beaten ornithologists. He has kindly allowed me to bring up a few examples* from this very interesting rubbish-heap, and from them I should be happy to demonstrate to anyone later on the efficacy of colour-pattern as a factor in generic differentiation. Time is too short now to give more examples, but there is a point which I should like to make here. It is this—that as a general rule there is nothing like so much intergrading between colour-patterns characterising genera as there is between such structural generic characters as the form and shape of the bill, the tail, or the wing. And this is just what we might expect; for naturally a highly specialised organ like the bill is constantly subject to minute structural changes in accordance with the functional uses to which it is put, and in correspondence with the type of insect-prey or other food which its owner is accustomed to capture or to feed upon.

Species are founded on colour, and one of the things which apparently we must not have is intergrading of the colour-factors characterising them. In genera, intergradations in, let us say, the form of the bill are apparently admissible. I give you as examples the variable form of the bill in the genus *Tringa* (the Redshank association), in the genus *Erolia*, or in the genus *Geospiza* from the Galapagos Islands, as now comprehended by Mr. Rothschild and Dr. Hartert.

* Examples of the following genera illustrating the subject were exhibited:—*Minla*, *Schœniparus*, *Pseudominla* (*Psittiparus*), *Lioparus*, *Yuhina*, *Ixulus*, *Alcippe*.

But why, I ask, fight shy of the very constant and congenital colour-pattern, so conspicuously characteristic of such genera as I have mentioned, and swallow the very variable structural forms of the bills, which have been impressed upon these various Eroliine or Tringine species through purely functional causes. Which is the oldest, the most constant, and the most fundamental character? Which is the most reliable character for the purpose of classification—one which had a direct and obvious relation with function, or one which had not such an obvious relation?

We get out of this dilemma by regarding the variations of the bill in the genera just noted as specific. But are we justified? I do not say we are not—but are we?

As a matter of fact, as I shall indicate later, my sympathies are, in many instances, with the lumper, but lumping genera on too large a scale may, perhaps, be almost as inexpedient a proceeding as splitting on too large a scale. To this subject, however, I shall return later.

(7) Colour-pattern as a phylogenetic clue.

In this connection, as is only natural, we turn to a consideration of the colour-pattern characterising the immature or nestling examples of any particular group selected.

I have here a very fine series of the nestling downy young of the Dunlin association—the subfamily formerly known as the Tringinæ, but for which I presume to think the term Eroliinæ might now be substituted, since the name Tringinæ is, by those who apply the principle of Linnean tautonymy, ruled out of court. As far as it goes, and I think it goes a very long way indeed, the colour-pattern common to all these nestling species serves as an excellent control experiment, whereby we are able to judge of the exact limits of the Eroliine subfamily. This colour-pattern, which I have not time to describe—you can see it for yourselves,—appears to be absolutely diagnostic of the subfamily. In it, we have a phylogenetic clue, pointing to the fact that in the Eroliinæ we have a very definitely differentiated group.

Compare this colour-pattern with the colour-pattern so very characteristic of the downy nestlings of the Redshank association—the Tringinæ,—and you observe at once a marked distinction. In the one case you have a spangled colour-pattern, in the other a striped one. I might add that in both series you have specific colour-tones superimposed on the fundamental subfamily colour-pattern. Incidentally, too, we glean that the Snipes are an offshoot from the Eroliine branch, while the Phalaropes are closely allied to the Redshank branch, as I have endeavoured to demonstrate by means of this diagram which I have drawn.

Here, again, in this box we have a series of downy young whose colour-pattern seems to be absolutely diagnostic of the Ringed Plover group or of the genus *Ægialitis*. This is what may be called a "True Plover" colour-pattern. Perhaps I can better explain what I mean by referring you to this diagram, which is a rough attempt to depict in a sort of bird's-eye view the phylogenetic relationships of the whole group of Waders. You will notice, for instance, that I have represented the main Limicoline stem as dividing into two branches—a Pluvialine branch and a Scolopacine branch. In the members of the Pluvialine or True Plover branch, we find the end of the bill, both in adult and nestling, ending in a distinct dertrum. In the Scolopacine branch there is no hint of a dertrum either in young or old. Corresponding with these distinctions, the colour-pattern characteristic of the nestlings of either group presents a well-differentiated colour-picture.

The Pluvialine branch, you will also notice, splits again into the Charadriinæ and the Vanellinæ (Lapwings and Wattled Lapwings), and if you compare the nestling young of these two groups you will again find a distinctive colour-pattern. For instance, the Ringed Plovers (*Ægialitis*) are differentiated from the Vanellinæ by not presenting a conspicuous pectoral band and by other minor points which I cannot now dwell on. But here you have two or three examples of the Vanelline subfamily.

But, it may be asked, of what practical use are all these facts, so far as they seem to go?

Well! Here is one example of how the colour-pattern and general appearance of the downy young may appear to settle once and for all a debatable point in generic relationship.

You will find in this box a nestling of a so-called Ringed Plover from Australia. In any of the classical works or catalogues you will always find this species included at the end of the list of species presumed to belong to the genus *Ægialitis*. The species I refer to is *Elseyornis melanops*, and, if you examine its nestling, I think you will agree with me that it certainly does not belong to the genus *Ægialitis*, but is worthy of the generic distinction which has been recently bestowed upon it.

Here is another instance, namely the downy young of *Oreophilus ruficollis* from southern South America. Dr. Bowdler Sharpe included the genus *Oreophilus* with the Wattled Lapwings; but if you compare this nestling species of *Oreophilus* with the nestlings of the Wattled Lapwings in this box, I think you will come to the conclusion that, whatever else this interesting and aberrant form may be, it is not a Wattled Lapwing. The colour-pattern is suggestively Eroliine, and the natural conclusion seems to be that *Oreophilus* is an aberrant Dunlin*.

The Ruff (*Machetes*), again, was placed by Bowdler Sharpe with the Tringinæ (Totaninæ olim), but the colour-pattern of the downy nestling is undoubtedly Eroliine in type, as anyone may see for himself by looking at the example in the front hall of the Natural History Museum at South Kensington, and comparing it with the type of colour-pattern characteristic of the Eroliinæ. The colour-pattern of the tail, tail-coverts, and rump in females and immature birds is also Eroliine—this diagrammatic drawing representing what I mean by the colour-pattern typical of the Eroliinæ. Judging, too, by this last character, *Micropalama* is Eroliine, while *Macrorhamphus* is Tringine.

* I am free to confess that there are almost, if not quite, as good reasons to look upon it as an aberrant Dotterel (*Eudromias*).

Again, the nestling young of *Chionis*, *Dromas*, *Œdicnemus*, *Hæmatopus*, *Recurvirostra*, *Thinocorus*, *Jacana*, and *Rhynchæa*, among others, are all extremely interesting from the point of view of the true phylogenetic relationships of these forms.

In attempting to construct this "family-tree" (exhibited at the Meeting), which purports to depict the phylogenetic relationships of the whole suborder of Waders, a study of the osteological characters of this group has been carried on simultaneously with a study of the nestling young (not to mention other aids to classification)—the result being that these two aids to the whole question of phylogeny have illuminated one another in the most interesting way.

But I must now hurry on to other groups of birds.

Here, for example, are some nestling Ducks of various genera, and, though I cannot pause to describe them individually, I may point out the very typical, constant, and well-differentiated nestling colour-pattern characteristic of such genera as *Tadorna*, *Glaucion*, *Nyroca*, *Œdemia*, and *Anas*—incidentally demonstrating to you how impossible it would seem to unite *Glaucion* and *Nyroca* under one genus, as has been recently done, or, on the other hand, to include the Ruddy Sheld-Duck in a genus (*Casarca*) distinct from *Tadorna*, since the colour-pattern characteristic of the nestling plumage of the Ruddy Sheld-Duck is identical with that of the Common Sheld-Duck. One may sum up by saying that the colour-pattern in the nestling Duck seems an even better guide to the differentiation of really natural generic groups than the colour-pattern in the adult, which last in its turn seems of more reliability than the generic characters usually depended upon.

Passing to Passerine examples, Mr. Swynnerton has kindly drawn my attention to the very suggestive resemblance which immature examples of *Tarsiger* bear to the young of *Erithacus*, as instanced in our own Robin. Here are some examples for comparison; and I think it might be held that the resemblance is even more than suggestive. *Tarsiger* at the present time is grouped with the Flycatchers, but it has Robin-like habits, and the types of colour-pattern of immature examples are so Robin-like that I think its position might well be reconsidered*.

Pœcilodryas is another genus included with the Flycatchers, but the young nestling of *P. capito*, with its very curious colour-pattern and aberrant feathering, is not in the least reminiscent of the young of this group. It recalls the fluffy plumage on the back of the adult *Corythocichla*—the Fluffy-backed Babblers. The young of *P. albifacies* presents the same peculiarities. The resemblance is so striking that it seems to me we might well ask ourselves—Is *Pœcilodryas* a Timeliine genus or a Flycatcher genus?

Again, it may be recalled that *P. æthiops*, from New Guinea, has always been included in the genus *Pœcilodryas*, although it bore the most suggestive resemblance to *Saxicola caprata* from India. Dr. Hartert has now removed it from its former genus to the genus *Saxicola*. Is it possible that in doing so he was in any way influenced, either consciously or sub-consciously, by the factor of colour-pattern?

In the case of *Pachycephala*, a genus belonging to the Laniidæ or Shrikes, we have an instance of the colour-pattern in the female giving a clue to true phylogenetic relationship: for *Pœcilodryas caniceps*, which was formerly regarded as a Flycatcher, we now find to be nothing more than the female of *Pachycephala gutturalis* (*P. obscurior* of Hartert). Was colour-pattern a negligible factor in arriving at this conclusion?

I might add that the young of *Pachycephala rufinucha gamblei*, from New Guinea, are well worth looking at from the point of view of phylogenetic relationships.

(8) The relationship of colour-pattern to the question of genera-splitting or genera-lumping.

In reality, the consideration of this aspect of colour-pattern follows naturally on the heels of the last, and, in effect, the few remarks which I shall have time to make

* Since this paper was read my attention has been drawn to the fact that Mr. Oberholser had already noted the same point (*cf.* Proc. U.S. Nat. Mus. 1915).

will take the form of a plea for some method by which we could combine genera, with the result that we should be able to recognise larger natural or phylogenetically allied groups, genetic phyla, super-genera, or whatever term we might like to apply to such groups. This, I think, could for the most part only be done by a systematic study of the colour-patterns characteristic of *immature* examples of whole groups of birds. Witmer Stone, in America, has already put in a plea to this effect. Briefly stated, my reasons for this plea are as follows:—

As things are now, in by far the larger number of cases, genera are purely artificial, arbitrary, and non-natural* groups which have been constructed for our convenience. They have, in fact, been constructed in order to simplify and codify our general concept of any particular family of birds.

Unfortunately, unless we simultaneously employ some method of integrating minor generic groups into larger and naturally constructed super-generic phyla, there seems to be a danger that, in the multiplication of genera which is now going on, our concept will be—not simplified, but complicated and obscured. For all practical purposes, we shall, in fact, have arrived by a laborious and painstaking process at the exact position from which we originally set forth. We shall indeed have been perambulating a circle; for we have only got to imagine the process of genera-splitting carried a few more steps further on and we shall have arrived at such a pass that all genera will have become *monotypic*. This may seem to be an exaggerated picture of the position, but if colour-pattern is really and truthfully ignored in generic classification—as systematists assure us—a flood of monotypic and quite artificial genera is not

* In the discussion which followed the reading of this paper, much was made of the idea that genera were non-natural, man-made and purely convenient groups. If however the units (species) of which genera are composed are natural, nature-made units, surely groups comprised of such units ought to be natural if only such units are properly assorted. If genera are not natural (and there is no question that many of them are not), that is the fault of those who created them—not Nature's. Personally I believe in groups of species which are genetically allied, that is to say I believe that Mr. Iredale struck the right note when he said that genera were or ought to be as natural as species.

an unlikely eventuality, so fine are the distinctions now drawn between trivial variations in the structure of the bill and other organs. If, on the other hand, colour-pattern is not ignored, genera-splitting is far less likely to do harm, and indeed is likely to be productive of much good, for we shall have got down to small groups of natural and genetically related species. These minor generic groups would in fact in most cases be found to consist of analytical varieties grouped around some central or dominant specific type. They would be really natural units which when integrated with others into larger and still natural groups (super-genera or what not) would express at a glance the phylogenetic natural relationships of the particular family or subfamily we were dealing with.

My point, therefore, is that while disintegrating within justifiable and natural limits we should at the same time integrate on the above lines.

Take, for example, the Redshank association again. In this group, so variable are the structural features of the bill and other anatomical features that almost every species could conceivably be made the type of a distinct genus; and the same might be said of the Dunlin association. Colour-pattern saves the situation.

Take, again, the case of the Ground-Finches of the Galapagos, famous for their association with Darwin's original conception of the origin of species! Mr. Rothschild, in conjunction with Dr. Hartert in a recent review of these Finches, has integrated them into one genus, *Geospiza*, sinking the three other genera (*Cactornis, Camarhynchus*, and *Platyspiza*) on account of the complete series of intergradations in the form of the bill which they allege to exist. Incidentally they hold that there are 34 species and subspecies of these Finches, while Mr. Ridgway maintains 35—in spite of the fact that there are only some 14 islands in the whole group, and that Duncan Island, which has a superficial area of some 12 square miles only, is found to contain no less than 10 of these species.

To me, with my limited experience, such a state of things seems to be rather shattering to one's preconceived ideas on the subject of species and their distribution. I have recently spent a considerable time over this group, chiefly from the point of view of colour-pattern, and my conclusion derived from this source is—that not only is there but one genus, as is maintained by Messrs. Rothschild & Hartert, but that there are but three or four species, instead of 35, and that these species were polymorphic. One of the things I did was to segregate all the examples of the ten Duncan Island species into one box, and then examine them from the point of view of intergradations in the form of the bill and colour-pattern. It was an interesting experiment, and, as I say, the only conclusion one could come to was the polymorphic nature of the two or three species, although it is conceivable that one or two forms may become, or are becoming, dominant, and may eventually become fixed.

I have instanced this case of the genus *Geospiza* because of the perfect series of intergradations in the form of the bill which are alleged, and because from that fact the common-sense view seems to be that we are here justified in lumping. On the other hand, here are three Icterine genera, *Trupialis*, *Leistes*, and *Sturnella* (or if we fight shy of *Sturnella*, let us say there are only two genera, viz. *Trupialis* and *Leistes*). Now in these genera there is a break in the continuity of intergradations in the form of the bill, and because of this break the rule is to consider these two forms as generically distinct; and here my point, which I fear is rather belated, comes in. If we examine immature specimens of these two genera, not only do we find the form and shape of the birds to be identical and with no break, but the colour-pattern is also identical; and the same may, I think, be said of *Sturnella*.

We have, then, in the colour-pattern presented by the immature examples of these forms a phylogenetic or generic link, yet, in the 'Catalogue of Birds,' *Leistes* is put into a distinct subfamily away from *Trupialis*. My point, therefore, is this—Can we not and ought we not to make use of such a link, or, rather, ought we not to have some way of expressing it so that we may be aware of it?

I am not advocating a policy of sinking or ignoring genera where obvious generic distinctions exist. That would, I think, be a very dangerous and regrettable policy. But I do think we ought to have some method of emphasising generic relationships *inter se*, by way of combining them into groups.

It may be answered that subfamily divisions already do this. But take the case of these five genera of the larger Caciques or Oropendolas. Here we have a very distinct group of the Icteridæ, well differentiated as regards structural generic characters, as regards specific characters, and as regards habits. For instance, in connection with the last, the Oropendolas only rear one chick, which presents peculiar characteristics, and it is only on very rare occasions that two eggs are found in their very peculiar nests.

They form, therefore, as I have said, a very distinct group, but, at the same time, it has been generally held by recent systematists that it is impossible to subdivide the family of the Icteridæ into subfamilies.

The obvious or logical conclusion, therefore, is that we ought to more often make use of super-genera by way of expressing or emphasising the near phylogenetic relationships of groups of genera.

That any real progress in this direction is retarded or rendered practically impossible is due to the fact that at present it is only on very rare occasions and quite sporadically that we find nestlings or immature examples of species represented in our collections.

Finally, if colour-pattern is going to be applied as a generic factor on anything like a large scale, it will, I am afraid, be found necessary to create many more genera or subgenera than exist now. But why not, if, and so long as, these genera or subgenera were found to be natural groups, corresponding, as I have found in many instances they do, with faunal areas or geographical regions or subregions; and if, and so long as, such subgenera or genera are integrated into larger natural groups, genetic phyla, or whatever term is employed, so that we may be aware of their natural relationships. These minor groups of birds are not like stamps, which are to be arranged methodically in an album. We have not finished with them when we have cleverly elaborated a system which ensures that we shall know exactly where to find them in the cabinets of a museum. On the contrary, they are natural groups of organic creations with independent organic histories and origins, with independent or particular areas of distribution, and doubtless with independent ecological life-stories. Are such things expressed or implied when we find in a recent and colossal work that no more can be done with a huge family like the Icteridæ than to write it down as one long continuous and tremendous list of genera, without analysis, without subdivisions or divisions, without a hint as to phylogenetic relationships or diversities, without an indication that, for all one can tell, judging solely by this method of classification, the first genus may not be closely allied in all respects with the last?

XVI.—*Mixed Bird-parties.*

By C. F. M. Swynnerton, C.M.B.O.U.

The occurrence of mixed bird-parties in the British Isles tends, I think, to escape notice to some extent through the fact that the intervening spaces are well filled up by scattered birds that are searching for their food independently.

In south-east Africa, through the relative scarcity of intervening birds, they are far more conspicuous, and they would appear to be equally so in portions of South America, to judge from Bates's fascinating description of "the associated bands of insect-eaters" of the forests of the upper Amazons. Here "numbers of distinct species, belonging to many different families, join together in the chase or search for food"; and "One may pass several days without seeing many birds; but now and then the surrounding bushes and trees appear suddenly to swarm with them. There are scores, probably hundreds of birds, all moving about with the greatest activity—Woodpeckers and Dendro-